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Analyses of sublittoral macrobenthic community change in a marine nature reserve using similarity profiles (SIMPROF)

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A B S T R A C T

Sublittoral macrobenthic communities in the Skomer Marine Nature Reserve (SMNR), Pembrokeshire, Wales, were sampled at 10 stations in 1993, 1996, 1998, 2003, 2007 and 2009 using a Day grab and a 0.5 mm mesh. The time series is analysed using Similarities Profiles (SIMPROF) tests and associated methods. Q-mode analysis using clustering with Type 1 SIMPROF addresses multivariate structure among samples, showing that there is clear structure associated with differences among years. Inverse (r-mode) analysis using Type 2 SIMPROF decisively rejects a hypothesis that species are not associated with each other. Clustering of the variables (species) with Type 3 SIMPROF identifies groups of species which covary coherently through the time-series. The time-series is characterised by a dramatic decline in abundances and diversity between the 1993 and 1996 surveys. By 1998 there had been a shift in community composition from the 1993 situation, with different species dominating. Communities had recovered in terms of abundance and species richness, but different species dominated the community. No single factor could be identified which unequivocally explained the dramatic changes observed in the SMNR. Possible causes were the effects of dispersed oil and dispersants from the Sea Empress oil spill in February 1996 and the cessation of dredge-spoil disposal off St Annes Head in 1995, but the most likely cause was severe weather. With many species, and a demonstrable recovery from an impact, communities within the SMNR appear to be diverse and resilient. If attributable to natural storms, the changes observed here indicate that natural variability may be much more important than is generally taken into account in the design of monitoring programmes.

1. Introduction

With an area of 13.24 km^2, the Skomer Marine Nature Reserve (MNR) surrounds the island of Skomer (Fig. 1), the smaller islands of Middleholm and Gateholm, and parts of the Marloes Peninsula in western Wales, UK. Water conditions range from relatively sheltered, deeper, waters north of the Marloes Peninsula, to shallow waters subject to extremely strong tidal currents. The waters and shores around Skomer Island have a long history of marine biological investigation, although few studies are reported in the peer-reviewed literature. Bassindale (1946) primarily described littoral communities around Skomer, although some sublittoral species, collected in dredgings from North and South Haven, were recorded. Hunnam (1976) provided some information on sublittoral infauna around Skomer, and a series of surveys in the 1980s mapped littoral and sublittoral habitats within the reserve (reviewed in Bunker and Hiscock, 1987). Following an initial quantitative survey of benthic communities in 1993 (Rostron, 1994) a subset of stations from this survey was selected for on-going monitoring (Fig. 1). These were quantitatively sampled in 1996, 1998, 2003, 2007 and 2009 (Rostron, 1997; Barfield, 1999, 2004, 2008, 2010).

Within a very widely-used framework for the nonparametric multivariate analysis of ecological data, Similarities Profiles (SIMPROF) analysis was described by Clarke et al. (2008) as, primarily, a way of testing for multivariate structure among samples. Recently Somerfield and Clarke (2013) demonstrated how Similarity Profiles analysis and other approaches may be combined to analyse associations among species, and to visualize those relationships. Type 2 SIMPROF determines whether observed associations could have arisen by chance. Type 3 SIMPROF detects statistically distinct subsets of species which respond to gradients in a coherent manner. How different groups respond is visualised using

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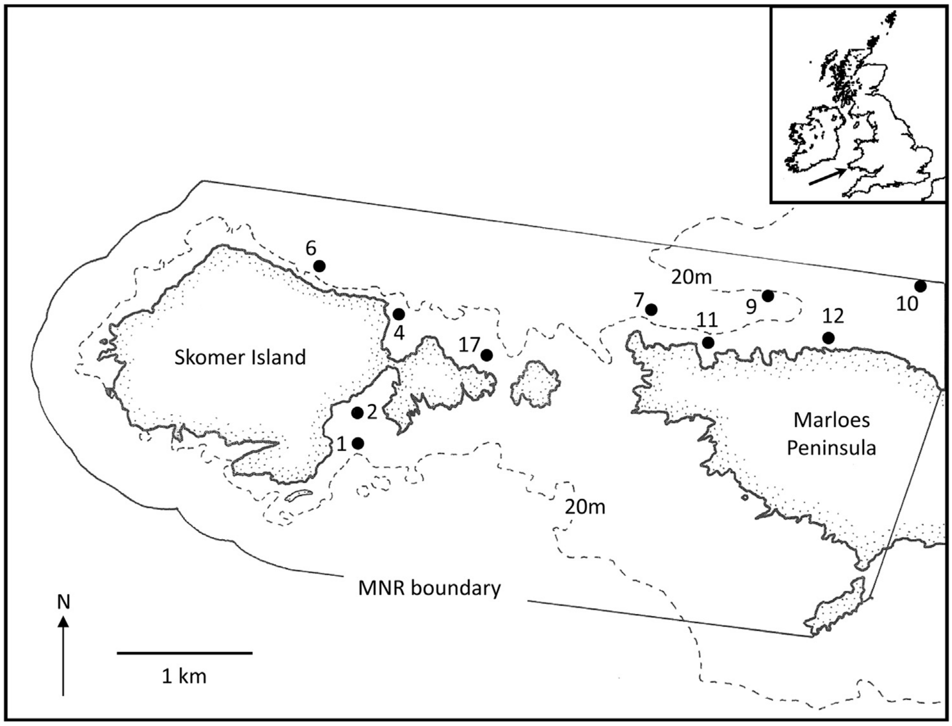

Fig. 1. Map of Skomer Marine Nature Reserve (MNR) showing sampling stations.

component line plots (coherent curves). The aims of this study are to use the various types of SIMPROF and associated methods to explore temporal variation in the benthic communities around Skomer over this 16 year period, and to consider the causes of observed changes.

2. Materials and methods

2.1. Field sampling

Although full details of the sampling and sampling analysis are given in the relevant reports (Rostron, 1994, 1997; Barfield, 1999, 2004, 2008, 2010) they may be briefly summarised as follows. Samples were collected in late autumn (October to November) using a 0.1 m^2 Day grab. Single samples were collected from 19 stations in 1993. 10 of these stations were selected for resampling in 1996 to represent a full range of variation in sediments and conditions (Fig. 1), when 2 or 3 replicate samples were taken. In later surveys (1998, 2003, 2007, 2009) 2 replicate samples were taken from each of the 10 stations. Large, readily visible organisms were picked out of each sample on deck, and the remaining sample was sieved on a 0.5 mm mesh and preserved in formalin for later analysis. A further grab was taken for sediment grain-size analyses.

2.2. Laboratory analyses

Animals in the samples were counted and identified to the lowest possible taxonomic unit (generally species). Quality control procedures, such as blind comparisons of samples, were generally conducted within later surveys and a reference collection of voucher specimens was maintained.

2.3. Numerical analyses

Samples collected from stations only sampled once, in 1993, were excluded from the analyses presented here. Prior to analysis taxa that were not identified to species, or that were only found as juveniles, were omitted. Replicate samples were pooled, so the numerical values in the data matrix are abundances of organisms 0.1 m^{-2}. Following a rigorous taxonomic standardisation, using taxonomic hierarchies from the UK Marine Species Directory (Howson and Picton, 1997) and the European Register of Marine Species (Costello et al., 2001), datasets were merged within the PRIMER package (Clarke and Gorley, 2006).

For Q-mode (sample) analysis abundances were fourth-root transformed and used to calculate Bray–Curtis similarities between every pair of samples. The resemblance matrix was clustered using hierarchical agglomerative clustering, and the resulting divisions tested using Type 1 SIMPROF. The matrix was visualised using non-metric multidimensional scaling ordination (MDS).

The focus of this paper is on temporal patterns in the MNR as a whole, so prior to inverse (r-mode) analysis abundances of each species were averaged within years. Variables were reduced by selecting only those species contributing at least 2% of total abundance in any one year. Annual abundances of each of the selected 33 species were standardised (converted to percentages of the total abundance of each species). A between-species resemblance matrix was constructed using the Index of Association (Somerfield and Clarke, 2013). The Index of Association (IA) takes the value 100 when two species have exactly the same percentage abundances across the samples (full positive association) and the value zero when they are found in completely different samples (full negative association). Defining y_{ij} as the abundance of the ith species ($i = 1, \ldots, p$) in the jth sample ($j = 1, \ldots, n$),

$$\mathrm{IA} = 100\left[1 - \frac{1}{2}\sum_{j=1}^{n}\left|\frac{y_{1j}}{\sum_{k=1}^{n} y_{1k}} - \frac{y_{2j}}{\sum_{k=1}^{n} y_{2k}}\right|\right]$$

Type 2 SIMPROF was used to determine whether species were associated with each other in terms of their numerical variation through the time-series. Species were clustered using hierarchical agglomerative clustering, and the resulting groupings tested using Type 3 SIMPROF to determine whether groups of species covaried coherently. Coherent curves (component line plots) were constructed to visualise how groups of species vary through time.

The analyses presented here were conducted using a developmental version of Primer 7 (α8), though all analyses may be undertaken using Primer 6 (see Somerfield and Clarke, 2013 for details).

3. Results

3.1. Variation in faunal composition among years, Q-mode analysis

38,458 organisms belonging to 683 species were retained in the dataset following data reduction. Type 1 SIMPROF confirms that there is significant multivariate structure among samples. Close examination of the dendrogram (Fig. 2) indicates a major division among sites at a similarity of 25–26%, which corresponds to a division between samples from >20 m (to the left) and those from <20 m (to the right). Within groups of samples for which Type 1 SIMPROF fails to reject a hypothesis of multivariate structure there is a tendency for samples from individual years to be clustered, rather than samples from individual sites. Ordination by MDS (Fig. 3) shows that samples from the 1993 and 1996 surveys stand out as being different from the rest, and the remaining surveys (1998, 2003, 2007, 2009) lie very close to each other. In general station-to-station differences in community structure were retained across years (Fig. 3), although there is a marked shift in community structure at Station 1 between 2003 and 2007. Since this corresponds to a known relocation of this station owing to sampling difficulties in 2007, data from this station are omitted from the following analyses.

Temporal patterns in part reflect variation in abundance and species richness (Fig. 4). There was a dramatic decline in abundance between the 1993 and 1996 surveys, though average abundances had recovered by 1998. There was a less marked decline in numbers of species between 1993 and 1996, but a marked increase in species richness between 1996 and 1998, with the higher level of species richness being sustained in later surveys.

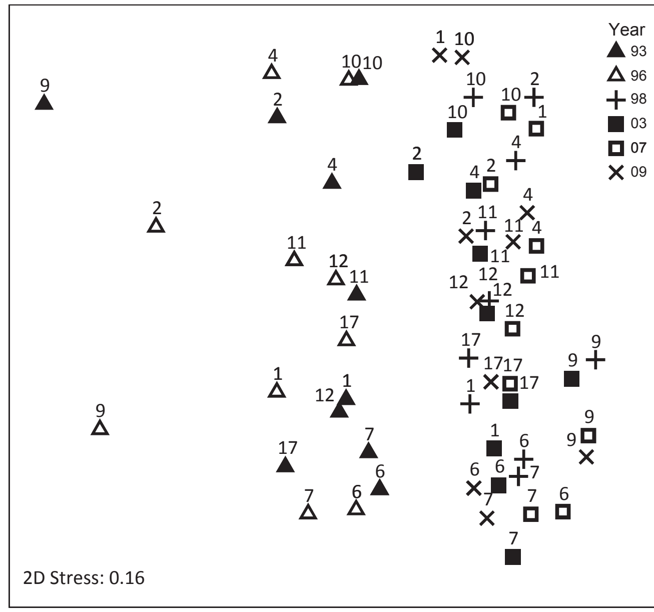

Fig. 3. Ordination by non-metric multidimensional scaling (MDS) of samples based on Bray–Curtis similarities calculated from fourth-root transformed abundances of macrobenthic taxa at each station averaged within years, labelled to highlight differences among years (symbols) and stations (numerals).

3.2. Taxa contributing to variation in faunal composition among years, r-mode analysis

Having established differences between years it is important to understand the nature of these differences in terms of the taxa

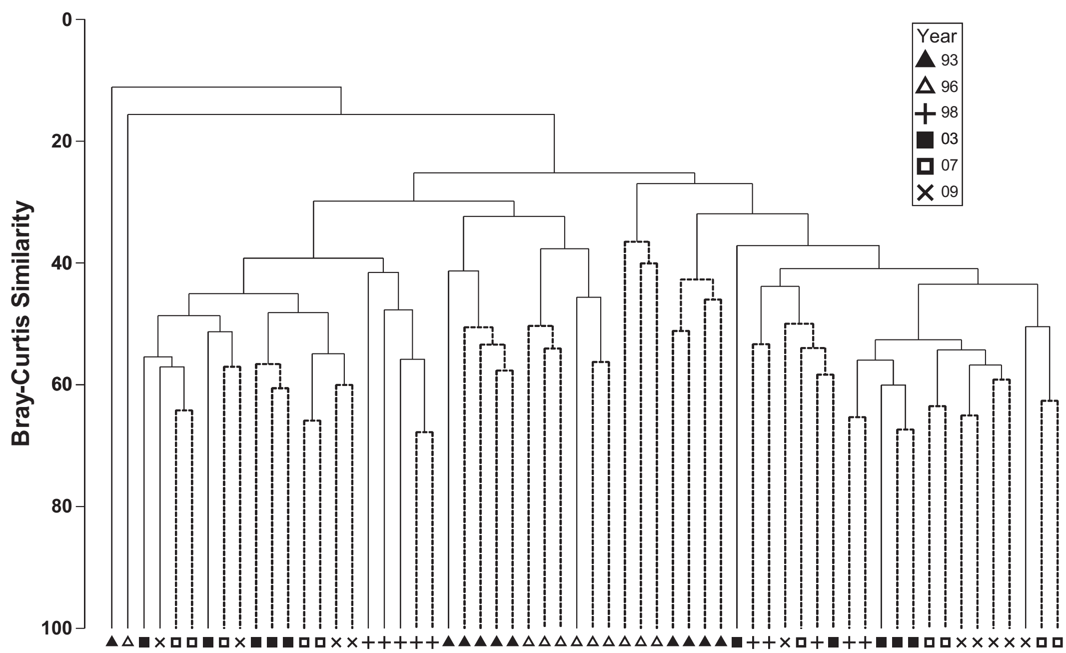

Fig. 2. Dendrogram derived by hierarchical agglomerative clustering with group-average linkage from Bray–Curtis similarities calculated from fourth-root transformed species abundances at each station averaged within years. Solid lines indicate significantly different samples and groups of samples ($p < 0.05$), dashed lines indicate groups of samples for which the null hypothesis could not be rejected ($p > 0.05$), as identified by Type 1 SIMPROF. Numerals indicate stations, symbols indicate years.

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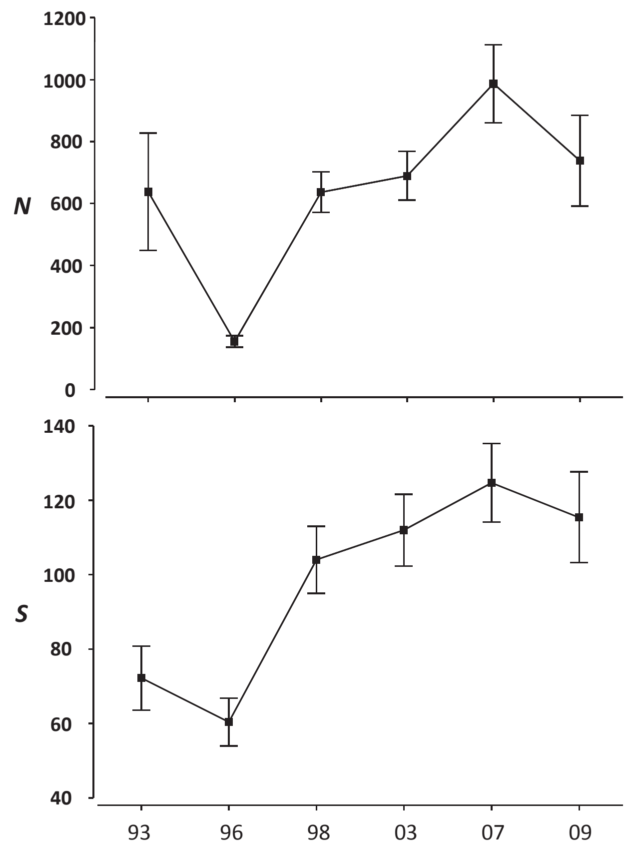

Fig. 4. Variation in within-station average numbers of individuals per 0.1 m^{-2} (N) and numbers of species (S) in samples. Means ± 1 s.d. plotted against the years in which data were collected.

involved. Type 2 SIMPROF assesses whether there are more, or less, species associated with each other (covarying) than would be expected if occurrences were essentially random. The results (Fig. 5) show that the observed value of π (4.3) is well outside the range of values which could have arisen if the null hypothesis, of no association among species, were true. Thus associations among species are significant. The Type 2 similarity profile (Fig. 5) shows that there is an excess of both lower-than-expected values of the IA (negative associations) and higher-than-expected values (positive associations).

Clustering of the species, with Type 3 SIMPROF tests at each node (Fig. 6), identifies 5 groups of species (A–F) which covary coherently among years. Coherent curves (Fig. 7) display these different patterns of variation. Species in Type 3 SIMPROF group A were relatively abundant in 1993, declined or disappeared by 1996, and showed at best only limited recovery in following years. Species in group B increased dramatically between 1993 and 1996, disappeared by 1998 and remained absent or only present in low numbers in following years. Group C consists of the single species *Abra alba*, which appeared in numbers in 1998, declined to lower numbers by 2003 but persisted in following years. Fluctuations in relative abundance of species in group D are characterised by variable abundance early in the time series, low abundance in 1998 and 2003, and then increasing abundance through 2007 and 2009. Species in group E were continuously present from 1998 onwards, generally increasing in abundance, while species in group F were absent in 1996 before increasing to a dramatic peak in abundance in 2007 from which they subsequently declined.

These variations in percent abundance may, in part, be explained by observed variations in sediment composition (Fig. 8). Species in group A (e.g. *Chamelea striatula* and *Ampelisca tenuicornis*) are typically found in finer sediments, and it is clear that the major change in sediments between the 1993 and 1996

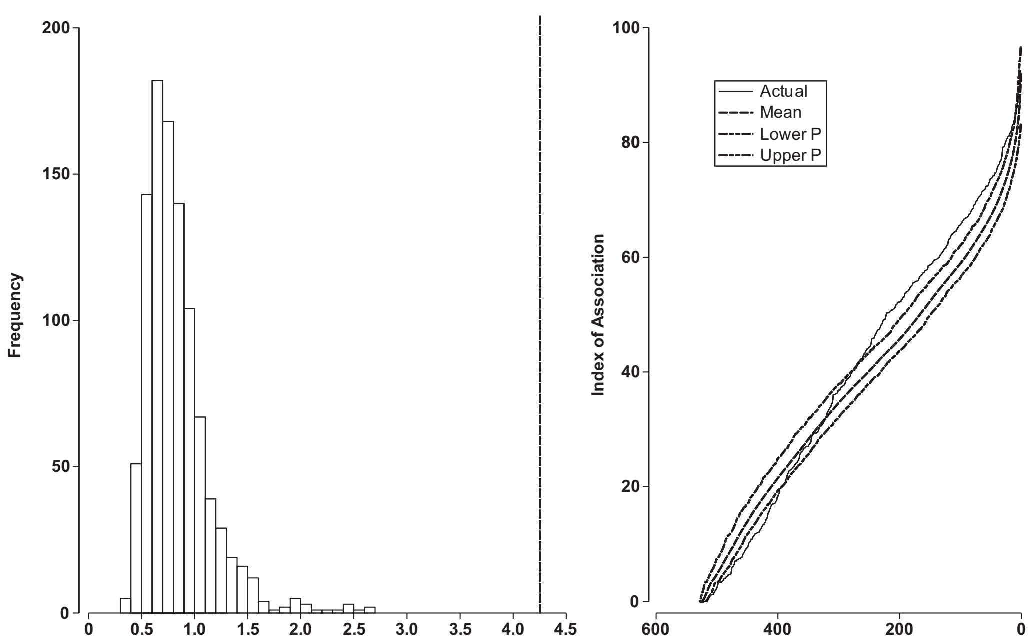

Fig. 5. Type 2 SIMPROF test based on index of association among the subset of 33 species which each contribute at least 2% to the average abundance in any one year. The observed value of the statistic π (4.3) falls outside the distribution of values generated by 999 permutations representing null-hypothesis conditions and is therefore highly significant ($p < 0.001$). In the Similarity Profile continuous lines denote the observed profile, the full set of pairwise resemblances ordered from smallest to largest (y axis) plotted against their rank (x axis). Dashed lines are limits within which 99% of resemblances would be expected to fall, for any given rank, under the null hypothesis of no association amongst species.

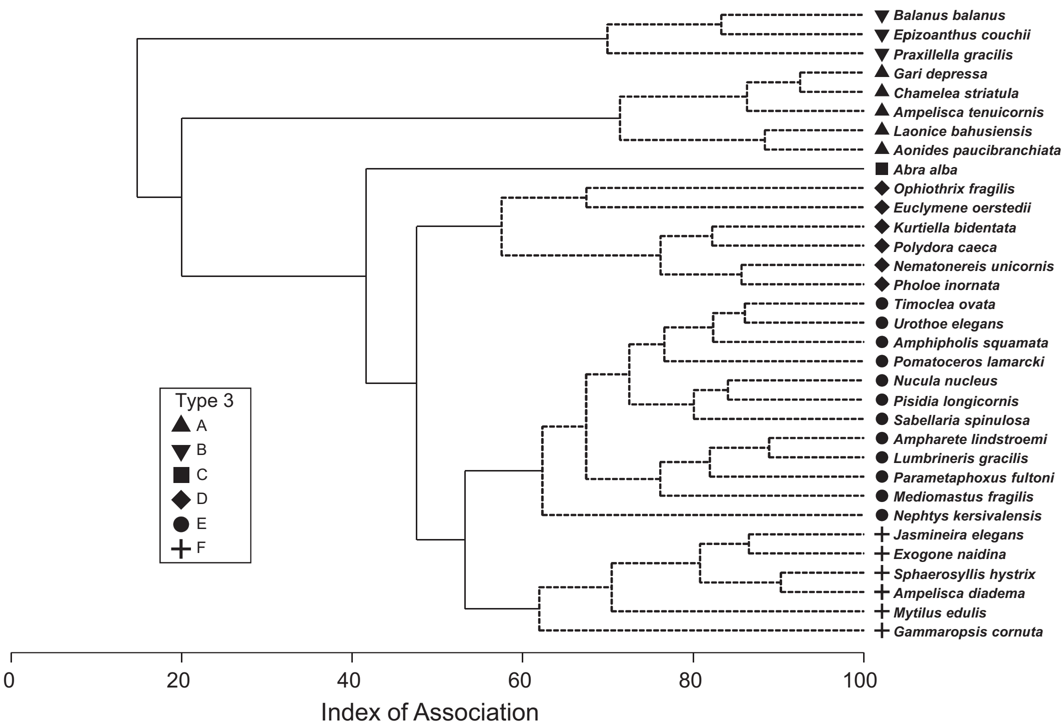

Fig. 6. Dendrogram from (r-mode) group-average clustering of the 33 'most important' species, based on the Index of Association among species, as in Fig. 5. Continuous lines indicate the 5 'coherent groups' (A–F) which were significantly differentiated by Type 3 SIMPROF tests (at the 2% level). Within each of these groups, the null hypothesis that all pairs of species have the same association to each other cannot be rejected, the subgroup structure identified by cluster analysis thus having no statistical support (dashed lines).

surveys was a decline in mud (silt and clay) content, and a shift to coarser sand and gravel. The increased sandiness of the sediments persisted in all the subsequent surveys. Species in group B (e.g. *Balanus balanus*) are typically found on coarse or mixed substrates, reflecting the peak in gravel content in 1996 (Fig. 8). *Abra alba*, constituting group C, is known to recruit in large numbers, which apparently happened in 1998, perhaps in response to space being made available by the decline in the

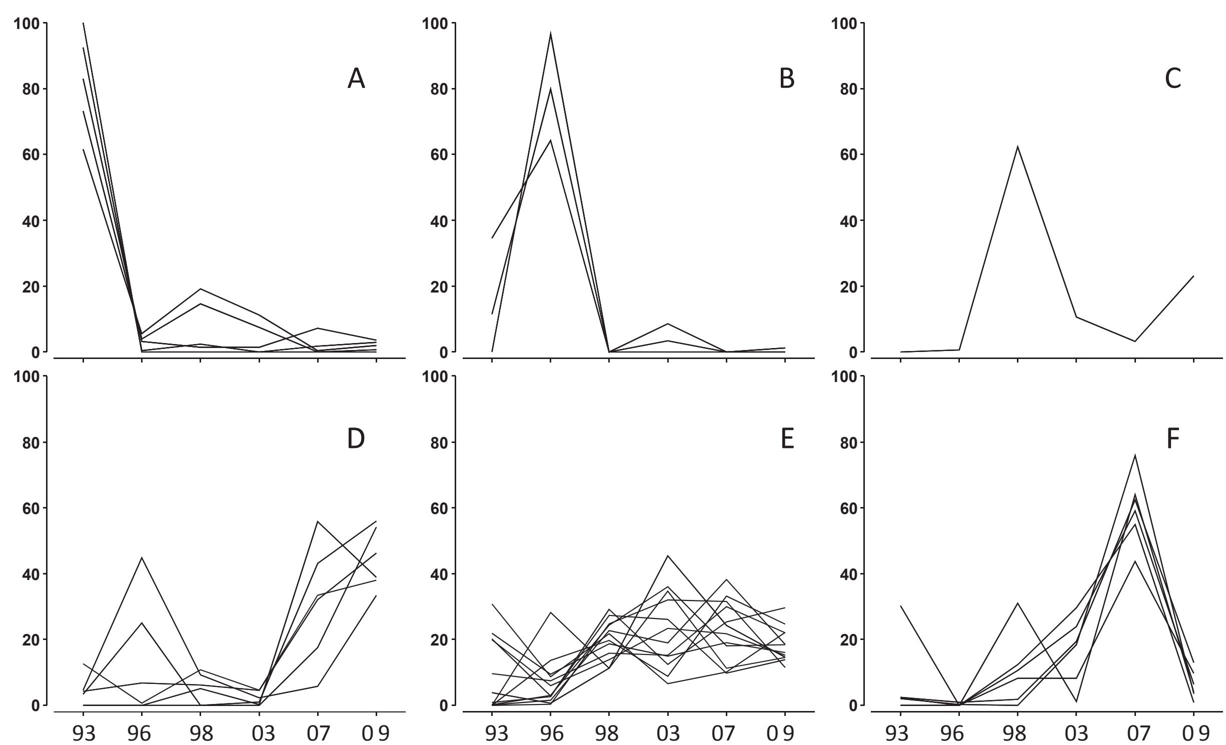

Fig. 7. Groups of 'coherent curves', namely component line plots for the groups of species identified in Fig. 6, showing the consistency of species responses within groups. The *y* axes are percentages of the total abundance of each species found across the 6 surveys (i.e. 'species-standardised', untransformed data). Species within groups are not individually identified because of their statistically inseparable responses.

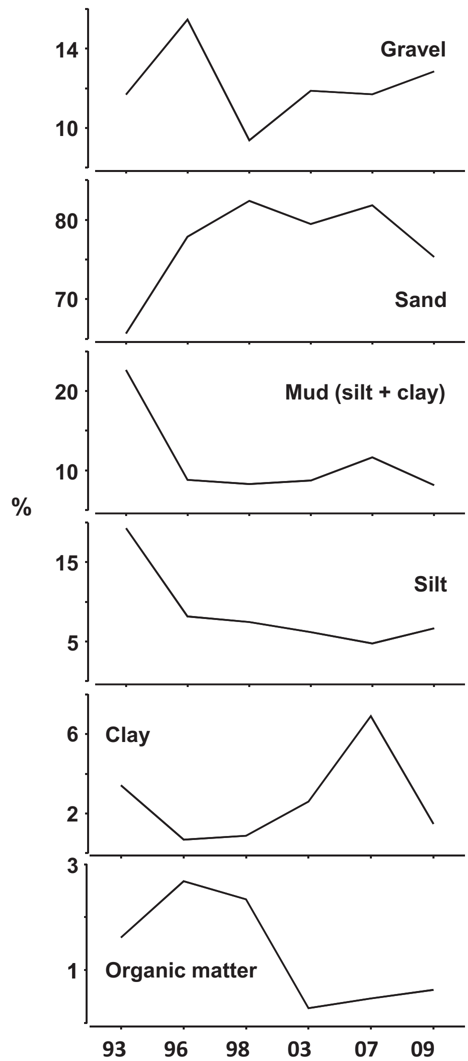

Fig. 8. Line plots of average percent contribution of different sediment fractions across years.

coarse sediment fraction and the generally sandier nature of the sediments. Group E species are typical of clean sands, though the slow increase in species' percentage abundance may reflect increasing sediment stabilisation and increasing habitat heterogeneity. For example, *Sabellaria spinulosa* is a potential stabiliser of sediments, *Pisidia longicornis* is known to be associated with *Sabellaria* reefs, and *Pomotoceros lamarcki* requires substrata such as shell on which to settle, though *Mediomastus fragilis* and *Nephtys kersivalensis* are more indicative of mobile clean sands. Species in group D are more likely to be found in mixed sediments such as stable shelly gravels. For example, *Pholoe inornata* inhabits empty shells, while *Dipolydora caeca* burrows within them. *Opiothrix fragilis* and *Kurtiella bidentata* indicate finer sediment, and it is possible that observed interplay between the clay and gravel content of the sediments (Fig. 8) reflects variation of abundance within this group. Species in group F (e.g. *Sphaerosyllis hystrix* and *Ampelisca diadema*) are also commonly found in sands, though the similarity in pattern with the clay content of the sediment (Fig. 8) is striking. These species were absent in 1996, so it is possible that the changes in sediment structure between 1996 and 1998 facilitated recruitment, and presence of clay in the sediment represents a proxy for sediment stability.

4. Discussion

Similarity Profiles (SIMPROF) analysis has a number of uses in the analysis of ecological community data (Clarke et al., 2008; Somerfield and Clarke, 2013). Here we show how Type 1 SIMPROF may be used to test hypotheses concerning structure among samples and may be useful in providing a stopping rule for interpretation of divisions imposed by a clustering algorithm. Type 2 SIMPROF (Somerfield and Clarke, 2013) assesses whether observed associations among species should be interpreted and indicates the nature (positive or negative) of those associations, while Type 3 allows the detection of coherently varying species. Coherent curves are used to visualise these coherent patterns in variation. We believe that these methods are a significant advance on other techniques, such as Similarity Percentages analysis (Clarke, 1993), used to examine variation among species (variables) and how this variation contributes to differences among samples. The major finding of the analyses conducted here are that major changes occurred in macrobenthoc communities inhabiting sediments within the Skomer MNR between surveys conducted in 1993 and 1996, assemblages shifted to a diverse but different state by 1998, and since then have remained relatively stable albeit with shifts in relative abundance of various species.

4.1. Possible causes of large interannual changes in faunal composition

Major storms battered the Skomer MNR in the weeks preceding the 1996 survey (Rostron, 1997). Waves >12 m high with a period of 15 s were reported on October 28. The factors determining sediment disturbance at depth by wind waves at specific sites involve a complex interplay between exposure, depth of the water column, tidal currents, sediment composition and surface roughness and biotic interactions (Hall, 1994), but it is likely that forces at the seabed were very destructive during the storm, at least at shallow sites (Rostron, 1997), leading to the observed major changes in community composition and sediment structure. That the sediments lost much of their mud content (Fig. 8) is consistent with the idea that fine sands may have been brought into the area by wave-driven resuspension and transport (Rostron, 1997), as is the fact that species in type 3 SIMPROF group A are those that typically inhabit muddy sediments. For example, it is known that among the tube-building Ampeliscidae all prefer poorly sorted sediment but different species have differing preferences, with *A. tenuicornis* preferring sediments with >16% mud (Parker, 1984).

Rees et al. (1977) described large changes in benthic populations and associated alterations in sediment silt–clay content associated with storm events in shallow waters on the northern coast of Wales, and storms have been shown to have marked effects on benthic community structure in similar communities elsewhere (e.g. Grémare et al., 1998; Labrune et al., 2007; Posey et al., 1996; Van Hoey et al., 2007). The removal of *Ampelisca abdita* tube mats by winter storms is part of the annual cycle in community structure off parts of the eastern coast of North America (Mills, 1969). Many amphipods, including Photidae and Ampeliscidae, are tube dwellers and their presence may enhance sediment cohesion and stability, and provide habitat for some species while excluding others (Mills, 1969). As mentioned above, the increasing trend in the percentage abundance of *S. spinulosa* may also have contributed to increasing sediment stability following the shift to sandier sediments in 1996, supporting the increase in percentage abundance of associated species.

Two other possible causes of observed patterns of variation merit consideration. On February 15, 1996, the tanker Sea Empress, laden with 131,000 t of crude oil and 2,400 t of heavy fuel oil, ran

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aground on rocks at the entrance of Milford Haven, only 12 km or so from Skomer. Over a period of time 72,000 t of crude oil and 360 t of fuel oil were released into the sea. Although much of this was dispersed into the water column by dispersants sprayed from the air, a sheen/oil mixture spread over a wide area, and quantities of oil came ashore within and adjacent to the MNR. Being winter, and during a period of high winds, the water column would have been fully mixed, and once oil was incorporated into the water-column it would easily have reached the seabed. High sediment loads of total hydrocarbons (up to 355 ppm) were found in North Haven (Station 4) on April 2, but levels subsequently fell (Rostron, 1997) and there is little evidence of any long-term (months to years) presence of elevated hydrocarbons in sediments within the MNR (Moore, 2006).

Among the species in Type 3 SIMPROF group A that declined or disappeared between 1993 and 1996 was *A. tenuicornis*. Ampeliscids are considered to be susceptible to oil pollution (Gesteira and Dauvin, 2000) and intolerant of even very low concentrations. Following the Amoco Cadiz spill ampeliscids disappeared from contaminated sediments and were slow to recolonize (Cabioch et al., 1982; Dauvin, 1982). Studies of benthic communities closer to the Sea Empress spill around Milford Haven (Rutt et al., 1998) showed reductions in abundances of amphipods and cumaceans, but no other notable effects on the macrofauna, or evidence of sustained contamination. The effect under consideration here is a general one, effecting almost all species and groups of species, so while the effects of the oil spill may be part of the explanation we consider this unlikely.

The Sea Empress incident was a very public affair, appearing on national and international news programmes and in other news media daily for weeks. Less public was a change that took place in 1995. As in most ports catering for large vessels, maintenance dredging is necessary to maintain navigable channels within Milford Haven and its approaches. Up to 1995 maintenance dredgings, primarily consisting of fine sediments, were regularly discharged at a disposal site 5 km or so off St Anne's Head, only 10 km southeast of the MNR. In 1995 the site was closed, and since then dredgings from Milford Haven have been taken to a new site some 20 km to sea for disposal. In 1993 many sites within the MNR had relatively high proportions of mud in their sediments, compared to later years (Fig. 8), which could reflect the cessation of import of fine material derived from dredgings, either as bed load or as suspended load. Thus the observed changes in assemblages could in part reflect longer-term changes driven by management decisions made some distance from the MNR.

4.2. The consequences of large changes in the context of monitoring

The trajectory of changes observed at Skomer suggests a single severe event followed by recovery. Storm-driven changes in community structure represent only one aspect of on-going natural variation. Interestingly, the changes observed at Skomer are similar in scale, extent and timing to changes observed in an *A. alba* community off the coast of Belgium (Van Hoey et al., 2007). Using a more extensive time-series they demonstrated that large-scale shifts in community structure, lasting several years, could be related to biological (recruitment) and physical (storms, sediment changes, cold winters) factors. Even in the absence of extreme events, the spatial structure of benthic communities may be highly variable (Armonies, 2000). Thus it may be that there is no need to seek a particular cause for observed variation, as it may simply reflect the natural ecological dynamics of the system. Few monitoring programmes take such potentially extreme variation into account in their design. As seen here, it is often impossible to unequivocally assign observed changes to potential causes of change, especially when those causes operate on spatial scales as large as, or larger than, the spatial extent of the monitoring survey. The idea that benthic communities are stable and persistent over long periods, in shallow sediments at least, is probably no longer tenable, and large shifts in community structure from one year to the next should not be considered surprising. Acknowledgement of such variability, however, is currently lacking within many marine conservation management frameworks. The purpose of monitoring in such frameworks is generally to determine measures and see if they are consistent with a target, or 'baseline' conditions. If they are, conservation objectives are being met and the feature being monitored may be considered to be in favourable status. As is shown here, variation of >50% in some measures may be entirely natural, which makes deciding what the baseline is, and detecting departure from it, potentially problematic. That being said, the Skomer MNR has consistently been shown to be in good condition and delivering its conservation objectives, despite the shifts in community structure described here.

4.3. Recovery, resilience and sediment monitoring in the Skomer MNR

It should be noted that the Type 2 and Type 3 SIMPROF analyses presented here are based on average community composition across the entire MNR in each survey. The Type 1 SIMPROF analysis (Fig. 2) shows that there is much more rich structure to explore, and a sensible next step in a full analysis might be to employ Type 3 SIMPROF within depth groups (>or <20 m for example), or indeed for individual stations, to explore temporal and spatial patterns.

The results presented here indicate that the sediment monitoring programme around Skomer is fit for purpose, as it could identify major changes in community structure and provide information about the nature and extent of such changes. The macrofaunal communities around the island are diverse, and resilient. It is to be hoped that the time-series will be maintained, not only to detect the effects of major events in the future but also to gain a better understanding of natural variability, and the biology of species, within these communities. Good quality benthic time-series are extremely rare and valuable, and where they have been maintained for 20 years or more they become important research tools (e.g. Dauvin, 1998, 2000; Frid et al., 2008; Warwick et al., 2002). Given that one of the stated goals of marine nature reserves is to provide opportunities for study and research, the maintenance and enhancement of this benthic in faunal time-series is a worthwhile activity above and beyond simply monitoring the state of the environment.

Acknowledgements

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Agreement number 308392) and Vectors (VECTORS of Change in Oceans and Seas Marine Life, Impact on Economic Sectors, Contract number 266445).

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